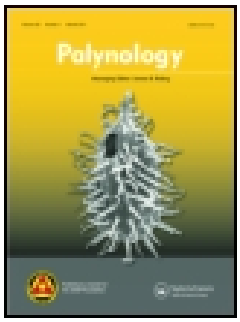

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A response "Comment to *Wetzeliella* and its allies — the 'hole' story: a taxonomic revision of the Paleogene dinoflagellate subfamily Wetzelielloideae by Williams et al. (2015)".

Graham L. Williams[a], Sarah P. Damassa[b], Robert A. Fensome[a*] and G. Raquel Guerstein[c]

[a]Natural Resources Canada, Geological Survey of Canada (Atlantic), Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2; [b] 119 South Street, Rockport, Massachussetts, USA 01966; [c]Laboratorio de Palinologia INGEOSUR, Departamento de Geologia, Universidad Nacional del Sur, Avda. Alem 1253, Cuerbo B´ 2do Piso, 8000 Bahia Blanca, Argentina

Abstract

The paper by Williams et al. (2015) concerning a proposed taxonomic revision of the subfamily Wetzelielloideae has led to a Comment by Bijl et al. (2016) that questions the validity of our assumptions regarding recognition of the equiepeliform, latiepeliform, hyperepeliform and soleiform archaeopyle types and their significance at the generic level. In this response we address the points that they raise, which are: the introduction of taxonomic criteria allegedly not followed in other fossil subfamilies; the erection of too many taxa; the unworkable nature of the proposed classification; and the reduction of stratigraphic applicability of many significant stratigraphic marker species. We have organized our response under the following topics: pragmatism versus theory; generic criteria: intergroup consistency; the genus *Apectodinium* and operculum attachment; stratigraphic utility; the number of taxa; and recognition problems. We also discuss specimens illustrated in the two plates included with the Comment. The variations in archaeopyle shapes and types of attachment of the operculum (the latter concept has been modified following more recent research) that we have used in part to separate the genera within the Wetzelielloideae have been previously applied to other

peridiniaceans subfamilies, most notably the Deflandreoideae. As with that subfamily, we consider that our focus on archaeopyle shape and operculum attachment for differentiating wetzelielloidean genera introduces an approach that may help refine the stratigraphic ranges of individual species. While it is a fundamental truth that there are no "correct" taxonomic ideas, we consider that new approaches should be tested with usage over time, not rejected out of hand prior to careful study.

Keywords: biostratigraphy; dinoflagellate cysts; evolution; Paleogene; taxonomy; wetzelielloideans

1. Introduction

Bijl et al. (2016) raise several objections to the new classification of the Wetzelielloideae that was presented in Williams et al. (2015), in which we emphasized the primary importance of archaeopyle outline and the secondary importance of wall morphology and ornamentation in distinguishing genera. The proposed reclassification led to the erection of thirteen genera and three species, a number which could be regarded as intimidating. In cataloguing their concerns in the abstract, Bijl et al. state that the proposed revision:

1. introduces taxonomic criteria that divert [diverge] drastically from criteria in other dinocyst subfamilies.
2. unnecessarily erects and emends many genera and species.
3. poses serious analytical and practical limitations.
4. leads to profound reduction of the stratigraphic applicability of many marker species.

Although Bijl et al. raise these four concerns in both the abstract and the introduction, they are not clearly organized in section 2 of their main text. In our response we have decided to follow a format that responds to the points raised above in a more logical fashion, albeit collectively addressing the issues raised.

2. Pragmatism versus theory

Bijl et al. (2016, p. 2*) entitle their Section 2.1 “Pragmatic versus hypothesized evolutionary lineages”, implying that our proposals are superficially based. But we deliberately did not propose any lineages in our paper and strongly discourage such an approach. As we suggested, dinocyst species interpreted from the fossil record represent tips of an “evolutionary bush”, and detailed attempts to arrange fossil species into lineages are, in our view, largely meaningless. What we did present (Williams et al. 2015, fig. 6) was an informal cladogram (and labelled as such) speculating on broad relationships among wetzelielloideans and focussing on archaeopyle type (further discussed below). As is well established and fundamental in the biological literature, cladograms reflect potential relationships, not lineages (Wiley et al. 1991). (*In writing this response the final pagination for Bijl et al.’s article was not available to us, so the page numbers we give are for the online version, which has pages numbered 1 to 7.)

The cladogram was added late to our paper as an afterthought at the prompting of a reviewer, so our generic classification was not driven by theory as reflected in that diagram. Indeed, our proposals are based on our long practical experience (Williams and Downie 1966; Damassa 1979; Bujak et al. 1980; Fensome et al. 2009; Weston et al. 2012; Fensome et al., 2016; Nøhr-Hansen et al. in press). We would be the last to claim that our extensive observations make our taxonomic ideas correct or better than others — indeed, taxonomy is a subjective discipline and no scheme can be considered “correct”. But our wealth of practical experience undermines the charge that our ideas are based on theory.

Although our proposed classification is founded on many years of incremental observations, the following anecdote helps emphasize the practical nature of our ideas. One of us spent several years analyzing Late Cretaceous and Cenozoic assemblages from the Scotian Basin, offshore eastern Canada (Fensome et al. 2008, 2009). Wetzelielloids are relatively common in many assemblages from Paleogene strata in the Scotian Basin, but it was puzzling that specimens with a clearly “popped-out” epeliform archaeopyle like those in Williams and Downie’s (1966) classic wetzelielloid study were rarely if ever observed; all Scotian Basin wetzelielloids showed a soleiform archaeopyle or no clearly evident archaeopyle. This mystery was dramatically underlined during a visit to view the Williams and Downie holotypes at the Natural History Museum in London; most if not all wetzelielloids in the latter material strikingly had an epeliform archaeopyle. It turns out that the Early Eocene is mostly missing in the Scotian Basin, probably stripped during the Montagnais impact event some 50 million years ago (Weston et al. 2012; Deptuck and Campbell 2012). Here then is a “first pass” practical biostratigraphic observation — wetzelielloids with an epeliform archaeopyle are primarily Early Eocene in age, whereas assemblages dominated by soleiform archaeopyles are of later Eocene and Oligocene age.

Bijl et al. (2016, p. 2) are concerned that "drastic revisions of the primary criteria for taxonomic classification … do not reflect phylogenetic significance." However, as further discussed below, we do not consider that our revisions are so "drastic": we just emphasized one factor, the archaeopyle shape, over others. Fensome et al. (1993) recognized that tabulation is a principal criterion in establishing phylogenetically based dinoflagellate taxa — indeed the primary criterion among dinoflagellate taxa represented in the fossil record. This tenet is now generally accepted. The problem among peridinioids is that the tabulation is so stable, with the "standard peridinialean tabulation" among fossil peridiniaceans (in contrast to protoperidiniaceans) varying little from the Late Jurassic to the Miocene (Fensome et al. 1993). The priority consideration in classifying fossil peridiniaceans has been the archaeopyle — both in terms of the number and configuration of plates involved and the shape of the second anterior intercalary (2a) plate, as discussed in detail below. The defining character of the Wetzelielloideae is the presence of a four-sided, or quadra, 2a plate, in contrast to the hexa, or six-sided, 2a plate of "mainstream" peridiniaceans. To us, the most reasonable basis for generic definitions would be to use aspects of tabulation if possible, to which end we applied the shape of the 2a plate as reflected in the archaeopyle. Thus, definitions of family, subfamily and genera all have a basis in the tabulation, and within the Wetzelielloideae this follows the precedent applied at least partially in other peridiniacean subfamilies. We accept that the shape of the wetzelielloidean 2a plate as shown by the archaeopyle may not reflect exactly the shape of the 2a plate in the motile cell (although no such motile cells exist to confirm this). However, in our experience, the configuration of the archaeopyle in wetzelielloideans correlates more with geological age than does the overall shape of the cyst.

Do Bijl et al. really consider that archaeopyle shape is potentially less reflective of phylogenetic relationships than horn development or ornament? Among fossil dinoflagellates, these features have been shown time and again not to accord with phylogeny. For example Cornu and Monteil in Monteil (1991) identified four morphological stages, or ecotypes, in the *Muderongia-Phoberocysta* complex based on variations in horn length, process type, and the distribution of ornament, including the extent to which it reflects tabulation. They showed that these morphological variations reflect environmental rather than evolutionary factors. The genera *Oligosphaeridium* and *Hystrichosphaeridium* were often considered to be closely allied in early work on fossil dinoflagellate cysts because of their strikingly similar chorate morphology. But Evitt (1985) convincingly showed by detailed examination of the process arrangement (reflecting tabulation) that the two genera belonged to different fundamental groups of gonyaulacoid cysts, recognized by Fensome et al. (1993) as the families Gonyaulacaceae and Goniodomaceae. These and other examples show that assessing phylogenetic relationships on the basis

of superficial shape and wall structure is fraught with problems. Aspects relating to tabulation have been proven generally not so susceptible to pitfalls of evolutionary convergence.

3. Generic criteria

According to Bijl et al. (2016, p. 1), Williams et al. (2015) introduced "… taxonomic criteria that divert [i.e. diverge] drastically from well-established conventions" and that (p. 4) a "profound concern for the field of dinoflagellate cyst paleontology" is that Williams et al. (2015) break with the "basic principle of hierarchy in morphological variation for the Wetzelielloideae …."

What exactly are the "well-established conventions" and the "basic principle of hierarchy in morphological variation" referred to by Bijl et al. from which we have diverged and broken? To assess this issue, let's look at the definitions of wetzelielloidean genera as established prior to Williams et al. (2015). The genus *Wetzeliella* itself was erected by Eisenack (1954, p. 187), who gave the following circumscription:

> "Shell more or less flattened, rhomboidal to pentagonal or also more or less oval, usually with apical horn, lateral horns on both sides and two antapical horns, all of which can be strongly reduced, without tabulation, almost always ornamented with bristles or spines. Transverse and longitudinal furrows, respectively, not determinable as flagellar groove (the former perhaps indicated sometimes). Ellipsoidal capsule present interiorly." (Translation from the German by Stover and Evitt (1978, p.130.)

An excystment opening (later termed an archaeopyle) was not recognized in 1954 by Eisenack, an omission remedied by Williams & Downie (1966, p. 182), who stated "Archaeopyle usually present … resulting from loss of plate 2a."

Gocht (1955) erected *Dracodinium* and *Rhombodinium*. *Dracodinium* was differentiated from *Wetzeliella* in lacking an apical horn on the pericyst, although there could be a slight protuberance. Subsequent authors (e.g. Williams & Downie 1966 by implication and Lentin & Williams 1976) considered *Dracodinium* to be a taxonomic junior synonym of *Wetzeliella*. But Costa & Downie (1979) and Lentin & Williams (1989) retained *Dracodinium*. Gocht (1955) differentiated *Rhombodinium* from *Wetzeliella* on its lack of ornamentation. Alberti (1961) considered *Rhombodinium* to be a subgenus of

Wetzeliella, but subsequent authors (e.g. Lentin & Williams 1977) retained *Rhombodinium* at generic rank.

The genus *Kisselevia*, although originally invalidly proposed (as *Kisselovia*) by Vozzhennikova (1963), was validated by Vozzhennikova (1967) (see Fensome and Williams 2004 for nomenclatural history). Vozzhennikova's (1963) concept appears to have encompassed forms that we would now consider as wetzelielloideans with a smooth or reticulate wall, with or without spinules "in modal connections" (based on translation in Stover and Evitt 1978, p. 110). Vozzhennikova (1967) restricted *Kisselevia* to forms with a reticulate or reticulate-spinose wall (based on translation in Stover and Evitt 1978, p. 110–111). Stover and Evitt (1978, p. 111) stated that "*Kisselovia* [i.e. *Kisselevia*] differs from *Wetzeliella* in having all or some of the intratabular groups of processes covered by pieces of ectophragm whose outlines approximate the shapes of paraplates." Stover and Evitt's concept was thus somewhat different from Vozzhennikova's, and after restudy of the type, Lentin & Vozzhennikova (1989) restricted the genus to forms with a reticulate periphragm and neither processes nor ectophragm. For wetzelielloideans with processes connected distally by trabeculae or ectophragm, Lentin & Vozzhennikova proposed the genus *Charlesdowniea*.

Lentin & Williams (1976) erected *Wilsonidium* for wetzelielloideans with sutural ornamentation. In the same year, Costa & Downie (1976) erected *Apectodinium* as a subgenus of *Wetzeliella* on the basis of a pericoel that was absent or restricted to the bases of the horns, a thin endophragm, identical periarchaeopyle and endoarchaeopyle, and an overall size less than other taxa within the *Wetzeliella* group (i.e. the Wetzelielloideae). *Apectodinium* was raised to generic rank by Lentin and Williams (1977). As *Apectodinium* has a pivotal place in the present discussion, we discuss it further in a separate section below.

The proposal of *Gochtodinium* by Bujak (1979) is especially significant in that it was the first genus in the group to be based on archaeopyle morphology, in this case a soleiform archaeopyle. However, Lentin and Vozzhennikova (1989, p. 219) stated that they could not accept a genus based solely on the presence of a soleiform archaeopyle. Oddly, in inadvertent support of our position, Lentin and Vozzhennikova additionally stated that "… it appears that the presence of a soleiform archaeopyle is an intraspecific variation which may be stratigraphically controlled …." Unrecognized at the time is that the type of *Wetzeliella*, an Oligocene specimen, also has a soleiform archaeopyle (RAF personal observation), and so we also consider *Gochtodinium* to be a taxonomic junior synonym of *Wetzeliella*. In

Fensome et al. (2009), the present authors erected two genera *Talladinium* and *Axiodinium*, based in large part on archaeopyle morphology.

Thus, prior to our 2015 paper, wetzelielloidean genera were based on a variety of criteria, ranging from wall structure to archaeopyle type, but we see no "well-established conventions" or "basic principle of hierarchy in morphological variation". And what do Bijl et al. (2016, p. 1) intend when they recommend that "we propose to retain the generic definitions of Wetzelielloideae that existed prior to the revisions by Williams et al. (2015) until a revision supported by the community is available". Which particular prior definitions do they mean? Presumably they would not accept the new genera (*Axiodinium* and *Talladinium*) proposed in Fensome et al. (2009).

In a similar vein, Bijl et al. (2016, p. 2) state:

> "Taxonomic definitions at the generic level are made predominantly based on specific morphologic and geometric features (such as cyst outline, cavation, number of wall layers, process outline and distribution, plate and/or sutural ornamentation, etc.), with the archaeopyle type being a consequence of geometry. Williams et al. (2015) broke with this convention because they specifically consider [sic] archaeopyle type to be an indicator for phylogeny."

On the contrary, using archaeopyle morphology to define higher level taxa (i.e. above species) seems to us a well-trodden path among dinoflagellate-cyst taxa. That archaeopyle morphology had largely not been used to define wetzelielloidean genera would seem more the exception to us. Tabulation is fundamental to higher-level classification among fossil dinoflagellates, but among forms with a similar overall tabulation, aspects of archaeopyle developments or its reflection in particular plates, has commonly proven critical, as demonstrated in Fensome et al. (1993). Take, for example, the goniodomacean genera *Homotryblium* and *Hystrichosphaeridium*. If one relied on ornamentation for generic differentiation, species of these two genera would be included in a single genus, with *Hystrichosphaeridium* being senior. However, the genera can be distinguished through the development of an apical archaeopyle in *Hystrichosphaeridium* and an epicystal archaeopyle in *Homotryblium*. Consider how much stratigraphic and paleoenvironmental information would be lost if the two genera were not separated (Dybkjaer 2004). Among the peridiniaceans, genera in the subfamily Deflandreoideae are widely defined by archaeopyle size and shape, a reflection of the nature of the second anterior intercalary (2a) plate. For example *Chatangiella* is defined by an omegaform hexa 2a plate, *Alterbidinium* by an iso-to stenodeltaform 2a, *Cerodinium* by an iso-deltaform 2a, *Deflandrea* by a

latideltaform 2a, and *Lentinia* by a very large isodeltaform 2a. These archaeopyle traits clearly have biostratigraphic, and surely evolutionary, significance. That the archaeopyle shape consistently reflects geometry is also belied by the fact that some specimens otherwise attributable to *Chatangiella* (with broad "shoulders") have a deltaform hexa archaeopyle, not an omegaform one (GLW and RAF unpublished observations).

Bijl et al. (2016, p.2) contend that we "applied the basic assumption that the archaeopyle type directly reflects the shape of the plate(s) involved", citing Harland (1982) as proof of this statement. However, Harland was studying protoperidinioids, which are notoriously variable in tabulation and archaeopyle development. While we accept that archaeopyles may not reflect the shape of equivalent plates on the motile stage in some cases, surely the archaeopyle type must to some extent reflect plate dimensions and shape. For example, it is hard to visualize a latiepeliform archaeopyle representing loss of a plate of identical dimensions to that of a hyperepeliform archaeopyle. And even if, for example, a soleiform archaeopyle does not exactly match the shape of the 2a plate in the motile cell, why could this not be a valid generic and phylogenetic criterion in itself, as its stratigraphic distribution clearly suggests to us that it is?

Another argument advanced by Bijl et al. is that the use of the archaeopyle splits otherwise identical taxa. For example, Bijl et al. (2016, p. 2) state that… "subtle differences in outline and ornament between *Charlesdowniea columna* and *Charlesdowniea coleothrypta* makes it difficult to separate them from one another …." In the context of the current discussion, Daniel Michoux (personal communication) has stated that he disagrees with Bijl et al.'s statement "… referring to the differences in outline and ornament between *Charlesdowniea columna* and *Charlesdowniea coleothrypta* as 'subtle'. As the author of *C. columna*, I consider the difference to be perfectly clear and these two species easy to distinguish." (Any future discussion about these two species should also involve the closely similar species *Wetzeliella*? *clathrata*, which we consider to have a soleiform archaeopyle.) In actuality our proposals should simplify differentiation, since the primary distinguishing feature would be recognizing whether the archaeopyle is equiepeliform or latiepeliform or, in the case of *Wetzeliella*? *clathrata*, soleiform. The problem of clearly separating species is widespread among fossil dinoflagellates and is equally true if criteria such as ornamentation, wall structure, pericoel development and the degree of expression of tabulation are involved; all have been used to define wetzelielloidean genera. Our revised concepts highlight this issue anew, but do not make it a greater or lesser problem in general.

Bijl et al. (2016, p. 4) make the sweeping statement: "We now observe very chaotic, inconsistent genus and species concepts, in which species with the same wall features are placed in multiple genera just because of a slight, non-diagnostic difference in archaeopyle type." This might be a valid criticism point if both *Charlesdowniea* (now *Piladinium*) *columna* and *Charlesdowniea coleothrypta* had the same stratigraphic distribution. However, a single specimen should never be used to determine the age of the assemblage. In such cases, if most specimens show one type of archaeopyle and its occurrence is consistent with the ranges of other markers in the assemblage, wouldn't it would be biostratigraphically useful to make the split based on archaeopyle style?

4. Intergroup consistency … or not?

Bijl et al. (2016, p. 2) end their section 2.1 with the confusing sentence: "Regardless of our concerns, the revision of taxonomic concepts to accommodate just one subfamily seems an illogical step if the taxonomic concepts applied towards the other dinoflagellate cyst groups remain the same." Their contention (p. 6) that "… the cyst-wall morphology [is] in practice a much more practical criterion for taxonomic differentiation than archaeopyle type, and more in line with that within other families" is in our experience untrue. Just as Evitt (1981) famously wrote "… dinoflagellates did it differently …", so each "group" within the dinoflagellates "did it differently" — one "size" does not fit all. (Bijl et al. mix "subfamilies" and "groups" in the quoted sentence; we will use "group" in the sense of any combination of genera that have been identified as constituting a family, subfamily or less formally recognized set of genera with similar morphology … for example, the areoligeraceans *Cyclonephelium*, *Tenua*, *Cerbia*, *Circulodinium*, *Cassidium*, *Canningia* and *Canninginopsis* could be considered the *Cyclonephelium* group.) Thus, for a group like the subfamily Palaeoperidinioideae, which expresses an extremely stable standard peridinialean tabulation, genera are defined on the number and arrangement of plates involved in archaeopyle formation. For example *Chichaouadinium* is based on the removal of the 2a plate and the incomplete separation of all surrounding plates, whereas *Palaeoperidinium* is based on the removal of all dorsal plates on the epicyst in a single opercular piece or as a flap adnate at the cingulum.

In the *Cyclonephelium* group, or indeed the family Areoligeraceae as a whole, not only is the tabulation extremely stable but so too is the nature of the archaeopyle; so for classification we have no choice but to resort to features of the wall structure and ornamentation for generic definitions. It seems obvious

to us that evaluating separate groups on their own internal merits leads to both a more practical generic breakdown and a potentially more phylogenetically meaningful one.

5. *Apectodinium* and operculum attachment

In Williams et al. (2015) we defined *Apectodinium* as wetzelielloidean cysts with an equiepeliform archaeopyle, periphragm and endophragm thin and appressed except sometimes under the horns, and a pericyst with processes that are distally free. To differentiate circumcavate, thicker-walled forms with an equiepeliform archaeopyle Fensome et al. (2009) erected the genus *Axiodinium*. Costa and Downie (1976, p. 608) considered *Apectodinium* to be "related to the original stock from which most other wetzelielloid species derived". The genus is an enigma. As noted by Bijl et al. (2016), the archaeopyle of *Apectodinium* can be variable, sometimes including the 4" plate and also sometimes being adnate. It is not surprising that if the 4" plate can be involved in archaeopyle formation in *Apectodinium*, that the operculum could be adnate.

In their critique of Williams et al. (2015), Bijl et al. place particular emphasis on *Apectodinium*, although this genus is atypical of the subfamily as a whole. The problem is perhaps that *Apectodinium*, as the probable precursor to other wetzelielloideans, was "experimenting" with the mode of archaeopyle formation. Similar experimentation is also shown by palaeoperidinioideans in the Albian to early Cenomanian, where otherwise morphologically similar genera such as *Luxadinium, Laciniadinium, Ovoidinium* and *Epelidosphaeridia,* show variability in the archaeopyle type and the presence of a free versus attached operculum.

In terms of attached versus free opercula, Williams et al. (2015) were incorrect in making the statement that the operculum in equiepeliform, hyperepeliform and latiepeliform archaeopyle types is always unattached. We now consider the degree of detachment of the operculum is variable, as demonstrated by Iakovleva (2016). Thus, we accept the modified definitions of the archaeopyle types proposed by Iakovleva, who emphasized that the soleiform type involves an archaeopyle formed by a generally inverted omegaform 2a plate, with the operculum consistently attached anteriorly. That cysts at various stages of excystment must be preserved explains why in some cysts an archaeopyle does not appear to be present.

There is obviously variability in the outline of the archaeopyle in *Apectodinium*, which is why we had difficulty in deciding how to fit it into the overall scheme. The specimens of *Apectodinium hyperacanthum* illustrated in Bijl et al. with the attached operculum would remain in *Apectodinium* following the redefinition of the epeliform archaeopyle by Iakovleva (2016). This emendation is also applicable to the hyperepeliform and the latiepeliform archaeopyle. But the soleiform archaeopyle is unique, again following Iakovleva's findings.

6. Too many new taxa?

One of the main criticisms that Bijl et al. (2016, p. 1)) make regarding Williams et al. (2015) is that the paper "… unnecessarily erects and emends many new genera and species." In fact, we proposed only three new species and did not emend any existing ones, but we acknowledge that 13 new genera is a lot for a single paper. The logic for creating so many genera was to provide a framework for testing the validity of the model in which we consider archaeopyle type as the first order hierarchical character. Our approach did not nullify the importance of surface ornamentation at the generic level; we did indeed use ornament type and arrangement, as well as wall structure, as secondary criteria.

7. Recognition problems

Another concern that Bijl et al. (2016, p. 4) express is that "The orientation of the cyst relative to the plane of view poses a serious limitation on the practicality of the proposed criteria underlying the revision." Well-orientated specimens are a key asset in species assignment, regardless of which morphologic features are diagnostic. This problem is demonstrated in the two specimens illustrated in Williams et al. (2015, pl. 1, fig. 15 and pl. 2, figs. 15–16); following previous criteria used to separate species of the wetzelielloideans, these specimens would be included in the same species, or at least the same genus. But taking into account the nature of the archeopyle, one specimen is assignable to *Sophismatia* (pl. 1, figs.15) and the other to *Sagenodinium franciscanum* (pl.2, fig.15–16).

Orientation to reveal key morphologic features is more of a problem in some fossil dinoflagellate genera than others. In the wetzelielloideans, the dorso-ventral compression of most specimens determines that when mounted on a slide, they will be orientated predominantly in that plane. If there is some doubt about one specimen, another specimen of the same species can be sought. Since ages are rarely

based on single specimens, this should not pose an insurmountable problem. Similar problems occur in other dinoflagellate-cyst taxa: witness the difficulty of confirming the identity of species of *Batiacasphaera* when they are orientated so that the archaeopyle looks precingular.

Recognition of wetzelielloideans that do not appear to have an archaeopyle can be frustrating, but usually a few with some indication of an opening can be found on a slide. There may be an explanation for this paucity of specimens in some samples that do not appear to have an archaeopyle. One possibility is that most or all of the specimens possess a soleiform archaeopyle and the operculum has fallen back into place. Another is that the sea floor in shallow marine paleoenvironments was anoxic, and therefore prevented excystment.

Regarding the specimen illustrated in Williams et al. (2015, pl. 1, fig. 2), Bijl et al. (2016, p. 4) state that "The oblique polar view results in an underestimation of the height of the archaeopyle relative to its width, giving the impression of an equiepeliform archaeopyle". A primary feature of the equiepeliform archaeopyle is that it does not extend into the apical pericoel, unlike the hyperepeliform archaeopyle. With this specimen, we thought that the archaeopyle did not extend into the apical pericoel, but we could have been wrong in our interpretation. Observations on other morphologically similar specimens in the same assemblage would solve this riddle.

Bijl et al. (2016) also objected to emphasis on archaeopyle type because it is difficult to consistently see the details of this feature. This can be due to: poor optical contrast; orientation; lack of penitabular or parasutural ornamentation; too many processes; partial adnation; some cysts not having excysted; quality of preservation; and the presence of obscuring debris. These are universal concerns in studies of all fossil dinoflagellate groups but can usually be overcome with patience in searching for other specimens.

8. Stratigraphic utility

Bijl et al. (2016, p. 1) state that our proposals will "... lead to profound reduction of the stratigraphic applicability of many marker species…." Firstly, Bijl et al. are confusing taxonomy with stratigraphy. And secondly, generic assignments rarely have an impact on stratigraphic ranges of species, with the exception of such species as *Wetzeliella articulata*, as discussed below. As Williams et al. (2015) did not generally modify species or species concepts, nothing has changed to affect stratigraphic ranges of most

of the species. Admittedly, the refinement of generic concepts will make some species more tightly constrained morphologically; for example *Wetzeliella articulata* should now have a shorter range than previously assessed, but this still has to be tested because the current generally published range is based in part on what we would now consider misidentifications. We fail to understand why tighter morphological circumscriptions leading to potentially more restricted stratigraphic ranges would be detrimental to biostratigraphy. The ranges of the bulk of wetzelielloidean species remain the same: no one would argue that, for example, *Apectodinium augustum* has a well-defined, restricted stratigraphic range (whether as *Apectodinium* or *Axiodinium*). What strikes us most is that the majority of species have not been transferred from their previous generic assignments.

Bijl et al. (2006, p. 1) fault Williams et al. (2015) for "…not introducing any new stratigraphic markers in replacement." However, the intent of our paper was not to introduce stratigraphic markers but to present a new taxonomic treatment for the Wetzelielloideae, emphasizing the variations in archaeopyle type.

We understand that it might be considered annoying to have to change generic names for species that are well embedded in zonation schemes. Does this mean that there should be a moratorium on taxonomic treatments of such names? In our view, wetzelielloidean taxonomy prior to our 2015 revision was not serving applications such as biostratigraphy well, and needed an overhaul using the full range of morphological criteria in a coherent and internally consistent scheme. We continue to think that our scheme, with thoughtful modifications such as those introduced by Iakovleva (2016), will achieve this goal if sincerely tested.

9. Comments on the plates of Bijl et al.

To substantiate some of their points regarding the supposed impracticability of the revisions to the Wetzelielloideae proposed by Williams et al. (2015), Bijl et al. (2016) include two plates; however, some of the specimens illustrated seem to be of questionable value in making their case. The specimens illustrated in Bijl et al. (2016, pl. 1, figs. 1–3) are all considered to belong to *Rhombodinium porosum* but apparently show variability in archaeopyle type ranging from "hypersoleiform to ?epeliform". The first problem is that Williams et al. (2015) used the term equiepeliform archaeopyle rather than epeliform archaeopyle. The second concern is that both the specimens shown in their plate 1, figures 1–2 have soleiform archaeopyles. Figure 3 appears to be latiepeliform. However, it is unusual in that the

operculum may still be attached but pushed into the endocyst. Are these three specimens from the same sample and is there any evidence of reworking? Their plate 1, figures 4–6 purport to show specimens of *Apectodinium* that possess an archaeopyle involving the 4" plate as well as the 2a plate. However, we do not find that plate 1, figures 4 and 5 convincingly show the involvement of the 4" plate. Moreover, the nature of the archaeopyle of the specimen illustrated in plate 1, figure 6 is difficult to determine. Plate 1, figures 7 and 8 are specimens of *Wetzeliella symmetrica*, the former with a soleiform and the latter with a "(slightly?) hypersoleiform archaeopyle" respectively. We consider that figure 8 shows a specimen with a soleiform archaeopyle. But regardless, it seems to be splitting hairs to regard it as "(slightly?) hypersoleiform". Figure 9 does not show a specimen with a posteriorly attached operculum but rather one with an anteriorly attached operculum.

Bijl et al. (2016) assign the specimens illustrated in plate 1, figures 10 and 11 to *Rhombodinium draco*, but state (in the caption, p. 3) that they "should be considered a (new?) species of *Rhadinodinium* according to Williams et al. (2015)" and that the "archaeopyle [in their figure 10] shows clear signs of rupture of the (likely) once soleiform archaeopyle. When it becomes questionable whether an operculum is secondarily ruptured or primarily attached/detached, speciation on a genus level becomes impossible if too much emphasis is given to the archaeopyle type for classification". First of all the authors are implying that one has to confirm the archaeopyle type in every specimen seen. Secondly, many genera among fossil dinoflagellates rely on recognition of the archaeopyle before they can be identified: examples are *Hystrichosphaeridium* and *Homotryblium*, *Exochosphaeridium* and *Pervosphaeridium*, and *Spinidinium and Chichaouadinium.* And some genera are difficult to name unless you have an apical or lateral orientation; an example is *Batiacasphaera*, which in most views, as noted previously, looks as though it has a precingular archaeopyle.

In their plate 2, Bijl et al. illustrate specimens "that do not clearly show an archaeopyle type and, therefore, are impossible to classify on the genus level using the proposed taxonomic concepts of Williams et al. (2015)." Again, how many times do you clearly discern an archaeopyle in a single specimen, even though it may be the key to its classification? The archaeopyle may not be developed because there was no excystment or it may be difficult to determine the type because of the orientation of the specimen, or because the operculum is partially attached (as highlighted by Iakovleva 2016) and has fallen back into place. Their plate 2, figures 1 and 2 are identified as *Apectodinium homomorphum*. This species tends to be common to abundant in samples, so determination of archaeopyle type should

not pose a problem. And under light microscopy, the thin-walled endocyst and its adherence to the pericyst, except where underlying the horns, would immediately reveal its identity.

We agree that, as illustrated, plate 2, figure 3 is impossible to speciate, although Bijl et al. label it as *Apectodinium homomorphum*. As we have stated above, this species is common in some assemblages, especially around the Paleocene–Eocene boundary, so finding specimens that show an archaeopyle should not be difficult in a productive sample. We think that the specimens illustrated in figures 4 and 5 have soleiform archaeopyles, but the quality of the illustrations precludes positive confirmation. Other specimens in the sample would probably provide the needed evidence. The operculum is not posteriorly attached, as it should never be in this category

Following Williams et al. (2015), we would include the specimen illustrated in Bijl et al.'s plate 2, figure 6 in *Vallodinium*, even though the operculum is still in place: that is because the 2a plate in this specimen is clearly equiepeliform. As Iakovleva (2016) has demonstrated, the operculum can be attached in the equiepeliform group. The archaeopyle of the specimen illustrated in plate 2, figures 7–9 and identified as *Wetzeliella symmetrica* looks latiepeliform. That being so, the specimen should not be in situ in the Oligocene and thus may be reworked. We wonder if there are any other specimens with similar morphology in the sample. One wonders how many palynologists would agree with the assignment of the specimens illustrated in plate 2, figures 4–5, 7–10 to *Wetzeliella symmetrica*.

10. Conclusions

Enhancing the stratigraphic and paleoenvironmental value of fossils are major goals of paleontologists, and most accept that taxonomy should be supportive of those pursuits while at the same time reflecting phylogenetic relationships insofar as possible. To achieve such a meaningful and internally coherent subdivision of a group (e.g. subfamily) a consistent hierarchy of factors is required, as is the need for flexibility of criteria between groups. That said, taxonomy should never be considered "written in stone"; taxonomy is a subjective pursuit, and no individual practitioner is obliged to follow the schemes proposed by colleagues (in contrast to nomenclature, which has definite rules that must be followed). Thus, Bijl et al. (2016) are free to use whatever taxonomic scheme they prefer. What is apparent and disappointing to us is that they wrote their paper opposing our long-considered ideas without trying them out — a few months is obviously not enough time to test what we agree is a new approach to the wetzelielloidean taxonomy. Moreover, they imply that they are speaking for a broader community,

writing (p. 1) that "… we propose to retain the generic definitions of Wetzelielloideae that existed prior to the revisions by Williams et al. (2015), until a revision supported by the community is available" [underline added here]. Who would be a member of the community that would give approval to any future taxonomic proposals for the Wetzelielloideae and what are the necessary qualifications for membership of said community? Of course it is the most fundamental tenet of science that ideas be reviewed, debated, and if necessary rejected. But in our view, taxonomic ideas need to be properly tested over time; and new ideas should be encouraged, regardless of whether or not they are eventually followed.

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12. References

Alberti G. 1961. Zur Kenntnis mesozoischer und alttertiärer Dinoflagellaten und Hystrichosphaerideen von Nord- und Mitteldeutschland sowie einigen anderen europäischen Gebieten. Palaeontographica Abteilung A. 116: 1–58.

Bijl P, Brinkhuis H, Egger L, Eldrett J, Frieling J, Grothe A, Pross J, Śliwińska K, Sluijs A. 2016. Comment to "*Wetzeliella* and its allies – the 'hole' story: a taxonomic revision of the Paleogene dinoflagellate subfamily Wetzelielloideae by Williams et al. (2015). Palynology. (available online).

Bujak JP. 1979. Proposed phylogeny of the dinoflagellates *Rhombodinium* and *Gochtodinium*. Micropaleontology 25: 308–324.

Bujak JP, Downie C, Eaton GL, Williams GL. 1980. Dinoflagellate cysts and acritarchs from the Eocene of southern England. Special Papers in Palaeontology, no.24: 100 p.

Costa LI, Downie C. 1976. The distribution of the dinoflagellate *Wetzeliella* in the Palaeogene of north-western Europe. Palaeontology, 19: 591–614.

Costa LI, Downie C. 1979. The Wetzeliellaceae; Palaeogene dinoflagellates. In: Proceedings of the 4th International Palynological Conference, Lucknow (1976–77), 2: 34–46.

Damassa SP. 1979. Eocene dinoflagellates from the Coastal Belt of the Franciscan Complex, northern California. Journal of Paleontology, 53: 815–840.

Deptuck ME, Campbell DC. 2012. Widespread erosion and mass failure from the ~51 Ma Montagnais marine bolide impact off southwestern Nova Scotia, Canada. Canadian Journal of Earth Sciences 49: 1567–1594.

Dybkjaer K. 2004. Morphological and abundance variations in *Homotryblium*-cyst assemblages related to depositional environments: uppermost Oligocene – lower Miocene, Jylland, Denmark. Palaeogeography. Palaeoclimatology. Palaeoecology 206: 41–58.

Eisenack A. 1954. Mikrofossilien aus Phosphoriten des samländischen Unteroligozäns und über die Einheitlichkeit der Hystrichosphaerideen. Palaeontographica Abteilung A 105: 49–95.

Evitt WR. 1981. The difference it makes that dinoflagellates did it differently. International Commission for Palynology Newsletter 4: 6–7.

Evitt WR. 1985. Sporopollenin dinoflagellates cysts: their morphology and interpretation. American Association of Stratigraphic Palynologists, Austin, Texas; 333 p.

Fensome RA, Williams GL. 2004. The Lentin and Williams index of fossil dinoflagellates 2004 edition. American Association of Stratigraphic Palynologists, Contributions Series, no. 42: 909 p.

Fensome RA, Taylor FJR, Norris G, Sarjeant WAS, Wharton DI, Williams GL. 1993. A classification of fossil and living dinoflagellates. Micropaleontology Press Special Paper, no. 7: 351 p.

Fensome RA, Crux JA, Gard IG, MacRae RA, Williams GL, Fiorina, F, Wach G. 2008. The last 100 million years on the Scotian Margin, offshore eastern Canada: an event-stratigraphic scheme emphasizing biostratigraphic data. Atlantic Geology 44: 93–126.

Fensome RA, Williams GL, MacRae RA. 2009. Late Cretaceous and Cenozoic fossil dinoflagellates and other palynomorphs from the Scotian Margin, offshore eastern Canada. Journal of Systematic Palaeontology 7: 1–79.

Fensome RA, Nøhr-Hansen H, Williams GL. 2016. Cretaceous and Cenozoic dinoflagellate cysts and other palynomorphs from the western and eastern margins of the Labrador–Baffin Seaway. Geological Survey of Denmark and Greenland, Bulletin 36: 143 p.

Gocht H. 1955. *Rhombodinium* und *Dracodinium*, zwei neue Dinoflagellaten-Gattungen aus dem norddeutschen Tertiär. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, no. 2: 84–92.

Harland R, 1982. A review of Recent and Quaternary organic-walled dinoflagellate cysts of the genus *Protoperidinium*. Palaeontology 25: 38–42.

Gocht, H. 1955. *Rhombodinium* und *Dracodinium*, zwei neue Dinoflagellaten-Gattungen aus dem norddeutschen Tertiär. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, no.2, p.84-92.

Harland, R. 1982: Recent dinoflagellate cyst assemblages from the southern Barents Sea. Palynology, v.6, p.9-18, pl.1-2.

Iakovleva KI. 2016. Did the PETM trigger the first radiation of wetzelielloideans? Evidence from France and northern Kazackhstan. Palynology, in press.

Lentin JK, Vozzhennikova TF. 1989. The fossil dinoflagellate cysts *Kisselovia* emend. and *Charlesdowniea* gen. nov. Review of Palaeobotany and Palynology, 58: 215–229.

Lentin JK, Williams GL. 1976. A monograph of fossil peridinioid dinoflagellate cysts. Bedford Institute of Oceanography, Report Series, no. BI-R-75-16: 237 p.

Lentin JK, Williams GL. 1977. Fossil dinoflagellates: index to genera and species, 1977 edition. Bedford Institute of Oceanography, Report Series, no. BI-R-77-8: 209 p.

Lentin JK, Williams GL. 1989. Fossil dinoflagellates: index to genera and species, 1989 edition. American Association of Stratigraphic Palynologists, Contributions Series, no.20: 473 p.

Monteil E. 1991. Morphology and systematics of the ceratioid group: a new morphographic approach. Revision and emendation of the genus Muderongia Cookson and Eisenack 1958. Bulletin des Centres de recherches exploration-production Elf-Aquitaine 15: 461–505.

Nøhr-Hansen H, Williams GL, Fensome RA. In press. Biostratigraphic correlation of the western and eastern margins of the Labrador–Baffin Seaway and implications for the regional geology. Geological Survey of Denmark and Greenland, Bulletin.

Stover LE, Evitt WR. 1978. Analyses of pre-Pleistocene organic-walled dinoflagellates. Stanford University Publications, Geological Sciences 15: 300p.

Vozzhennikova TF. 1963. Klass Peridineae (Dinoflagellateae). Peridinei, ili dinoflagellaty. In: Kiselev A, editor. Tip Pyrrophyta. Pirrofitovye Vodorosli; In: Vakhrameeva VA, Radchenko GP, Tachmadzhana AL, editors. Tip Pyrrophyta. Pirrofitovye Vodorosli. Vodorosli, Mochoobraznie, Psilofitovie, Plaonovidnie, Chlenistostebelnie, Paporotniki; In: Orlov A., editor, Osnovy Paleontologii, 14: 171–186.

Vozzhennikova TF. 1967. Iskopaemye peridinei Yurskikh, Melovykh i Paleogenovykh otlozheniy SSSR. 347 p; Izdatelstvo Nauka, Moscow, U.S.S.R.

Weston JF, MacRae RA, Ascoli P, Cooper MKE, Fensome RA, Shaw D, Williams GL. 2012. A revised biostratigraphic and well-log sequence-stratigraphic framework for the Scotian Margin, offshore eastern Canada. Canadian Journal of Earth Sciences 49: 1417–1462.

Wiley EO, Siegel-Causey D, Brooks DR, Funk VA. 1991. The compleat cladist. A primer of phylogenetic procedures. University of Kansas Museum of Natural History, Special Publication 19: 158 p.

Williams GL, Downie C. 1966. *Wetzeliella* from the London Clay. In: Davey RJ, Downie C, Sarjeant WAS, Williams GL. Studies on Mesozoic and Cainozoic dinoflagellate cysts; British Museum (Natural History) Geology, Bulletin, Supplement 3: 182–198.

Williams GL, Damassa SP, Fensome RA, Guerstein GR. 2015. *Wetzeliella* and its allies — the 'hole' story: a taxonomic revision of the Paleogene subfamily Wetzelielloideae. Palynology 39: 289-344. (Published online 2015, hard copy 2016.)